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MORPHOLOGICAL STUDIES OF THE THORAX OF THE ANT¹

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Several excellent studies have been made by various workers on the thoracic structure of insects, particularly of the Hymenoptera. Few of these, however, have dealt specifically with the thorax of the Formicidae. Many of the figures of the Formicoid thorax that are present in the literature are of little anatomical value since they illustrate the general shape rather than the detailed anatomy. In the absence of any recent or complete work on the thoracic structure of the Formicidae the following study was made. Its purpose was to interpret the thoracic structure of the group in the light of our present knowledge.

Many investigators have shown the value of a study of the thoracic sclerites in determining the phylogenetic relationships of the various orders and families of insects. Accordingly, some consideration of the phylogenetic relationships of the seven subfamilies of ants based on the thoracic structure is given here.

The Formicidae may be easily divided into two general groups, the fertile winged and the sterile wingless castes. The embryological studies of Dewitz (1878) have shown that in their ontological development the sterile workers possess well developed wing buds

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which usually disappear upon the attainment of the adult condition. This is convincing evidence that the wingless forms were at some period in their phylogenetic development descended from winged forms, and the occasional appearance of winged workers substantiates this conclusion. To trace the development of the wingless form, it is first necessary to study the structure of the winged forms and then trace through a series of intermediate forms to the wingless type. (Tulloch, 1930, a, b.) In this way the modifications of the various sclerites can be traced to determine which persist and compose the body structure of the worker. The region of the body most indicative of change from the winged to the wingless type is the thorax since the loss of wings and their accompanying muscles has a profound influence on the simplification of this region during the adoption of the terrestrial habit.

REVIEW OF LITERATURE DEALING WITH THE FORMICOID THORAX

That the thorax of the ants is composed of four segments and not three as in most insects was recognized by some of the earliest investigators. Ratzeburg (1832) working with the larvae of Hymenoptera, particularly of the genus *Formica* maintained that the fifth segment of the larva forms, not the so-called "scale" or first abdominal segment, but the hinder part of the thorax. This view was also maintained by Audouin (1820) and Latreille (1820), while, on the contrary, others such as Kirby and Spence (1822-26) and Macleay (1830) considered the thorax of these insects to be composed of three segments, as usual. Burmeister (1836) and Westwood (1840) also agreed that the thorax of the ants was composed of three segments.

Newport (1839) stated that "at first we were inclined to Audouin's opinion, more especially on account of what we shall presently find in Lepidoptera, in which the fifth segment, in its atrophied condition, is as much connected with the thorax as with the abdomen. On further examination, however, we are satisfied that the portion of the metathorax which is posterior to the incisure belongs to the third segment of the thorax."

In 1877-79 John Lubbock detailed accounts on the internal and external structure of the ant thorax. He followed the opinions of the earlier workers, Latreille, Ratzeburg, exponents of the four segment theory. The criterion used by Lubbock was the number and position of the spiracles. He noted that in the ants there were

three pairs of spiracles, the first two pairs being between the pro- and mesothorax and the meso- and metathorax, corresponding to the two pairs of thoracic spiracles of other insects. The third pair of spiracles, those of the first abdominal segment, Lubbock considered to be on the side of the metathorax, or in the margin between the metathorax and the first abdominal segment of other insects. Burmeister, writing earlier than Lubbock, considered that the ants have only two pairs of thoracic spiracles, those between the pro- and mesothorax and those "on the metathorax itself." Lubbock, however, suggested that Burmeister failed to identify "the meso-metathoracic spiracles" and showed that in *Lasius flavus* they exist and are easily recognizable. As a general rule, Lubbock's assertion that the thorax of ants bears three pairs of spiracles is correct; yet in certain ants the meso-metathoracic spiracles are either absent or so completely reduced that they are not discernible even upon careful microscopic examination.

The opinion expressed by Lubbock and suggested by earlier workers that the thorax contained a modified abdominal segment was, in substance, correct. Specifically, their views concerning the limits of the metathorax and the first abdominal segments, as determined by the spiracles, were incorrect. Their confusion was perhaps due to the fact that they did not readily recognize that the thoracic spiracles are intersegmental while the abdominal ones are intrasegmental.

Nassonoff (1889) was one of the first to consider the structure of the ant thorax in any detail. He selected for study the queen of *Lasius flavus* and made many excellent illustrations. His interpretations were in accord with the views of the time, but somewhat different from the ideas of the present time.

Janet's (1898) work on the thorax of the queen of *Myrmica rubra* is of signal importance because he disassociated the parts of the thorax and showed the relations of the regions to each other. Both Nassonoff and Janet recognized the true limits of the first abdominal tergite and of the metathorax, but their views relative to the limits of the sternal regions were mistaken.

Perhaps the greatest contribution to the knowledge of the thorax of the Formicidae was that made by C. Emery in 1900. Realizing the great confusion in the interpretations of the thoracic sclerites, he attempted to homologize the various structures in the different castes of ants. More especially he showed the manner in which the fusion of sclerites took place in the posterior region of the thorax, and in what measure the epinotum and the meta-

thorax participated in the formation of the so-called metathorax of other authors. His interpretations have been subsequently adopted by Wheeler (1910), Donisthorpe, (1914) and others in their treatises upon the ants, and by nearly all myrmecographers in their description of novelties.

Emery selected as a generalized form the male of *Streblognathus aethiopicus*, a large Ponerine common to South Africa. In the pleural and notal region it is as completely sutured as many of the higher Hymenoptera.

For a study of the notal region of the thorax, *Paraponera clavata* was selected. In general, the interpretations he gave were correct, but in regard to the limits of the sternum and certain notal regions, several misconceptions have been noted.

By examining a series of *Paltotyreus tarsatus* from the winged female to the wingless worker through the intermediate ergatoid, an attempt was made to show how fusion of the sclerites may have taken place after the deprivation of wings. The study of this particular series, inadequate as it was, was the first attempt to homologize the sclerites of the winged and worker ants by a serial morphological study.

After a consideration of several other Ponerine forms, Emery showed the relationship of the other subfamilies to the Ponerinae, basing his conclusions on the characters of the workers. By using the position and nature of the spiracles as pertinent characters, he showed that the Dorylinae and the Myrmicinae are easily reducible to the Ponerinae, likewise, he considered the Dolichoderinae to be directly connected to the Ponerinae through the genus *Aneretus* and the Camponotinae to be directly connected to the Dolichoderinae.

Snodgrass (1910) in his classic work on the Hymenopteron thorax considered the ants briefly. He pointed out the true limits of the sternal region as well as true relationships of the notal regions. His work has provided a foundation for subsequent workers in any group of the Hymenoptera since he considered all the various types.

The investigations of Crampton (1909, etc.) have added much to the knowledge of the thoracic structure, especially in the more specialized groups of Diptera and Hymenoptera.

METHOD

All the specimens were studied in a liquid medium (water, glycerine, alcohol) with the aid of a binocular microscope, the field of which was illuminated by two powerful spotlights. In many

cases the specimens were boiled in a 10% caustic potash solution and then the internal tissues washed out with running water, thereby making the sclerites show up more clearly and also making dissections of different sclerites possible. The drawings were made with the aid of a cross-line ocular micrometer disc and graph paper. By this procedure accurate relationships of the various sclerites were obtained.

DESCRIPTION OF A TYPICAL FORMICOID THORAX

Morphologically the thorax of the Formicidae is formed by the first four postcephalic segments. The first three of these, prothorax, mesothorax and metathorax, are characterized by the presence of legs, and together constitute the true thorax. The fourth segment, the propodeum, commonly referred to in the ants as the epinotum (known also as the median segment and erroneously as the metanotum) is the tergite of the first abdominal segment, which has been fused with the metathorax and become completely incorporated into the thoracic region of the body. Before attempting a comparative study of the Formicoid thorax it is necessary to become thoroughly acquainted with the thoracic structure in one of the more generalized members of the family. Since the Formicidae is perhaps the most specialized family of the Hymenoptera, and therefore of all insects, the structure of a selected generalized form is exceedingly complex. The original structure is so obliterated, while secondary characters are so prominent, that erroneous conclusions may be drawn if attention to other less specialized groups is not given. In order to avoid misinterpretations of the thorax of the less specialized ants such as *Paraponera*, a preliminary study of lower Hymenoptera such as *Xiphidrya*, *Ampulex*, *Polistes* and others was made. In addition, particular attention was given to the investigations of Snodgrass (1910) who worked out the homologies of various sclerites especially among the non-aculeate forms, and Crampton (1914, 1926) and Martin (1915) who made important contributions to the knowledge of the sclerites found in the cervical regions and in the tergum.

The thorax of *Paraponera clavata* was selected as representing a generalized condition of the ant thorax. *Paraponera clavata* is a desirable laboratory paradigm because of its large size, and its yellow color does not obliterate the limits of the sclerites. As with many specialized groups of insects, the limits of many of the sclerites have become obliterated, and in such cases the terms applied are connotative of general areas rather than of definite sclerites.

Prothorax (Pl. VIII, figs. 1, 2, 4). The pronotum (PN) is a large, broad, transverse plate situated on the lower anterior portion of the thorax. It extends laterally to the mesopleura and its dorsal posterior angles which are more or less broadly rounded form lobes which cover the mesothoracic spiracles lying underneath on the anterior margin of the mesepisterna (ANE). The ventral posterior angles are definitely pointed and extend underneath the thorax and nearly meet ventrally at the anterior margin of the mesosternal region (PN). The front margin of the pronotum covers the points of attachment between the head and the internal occipital processes (OP) of the latero-cervicals (LC). The hind margin is concave and covers the prephragma (PHG) of the mesonotum. The two large latero-cervical plates (LC) form the greater portion of the wide, flat, antero-ventral surface of the prothorax. Each latero-cervical is produced antero-laterally to form a portion of a narrow, collar-like transverse band from the inner surface of which projects a sclerotized tooth called the occipital process (OP) on which the head articulates. Near the lateral posterior angle of each latero-cervical there projects from the inner surface a hook-like structure known as the coxa process (CXP). The lateral portions of the latero-cervicals are curved sharply upward and extend under the pronotum a distance equal to one half their width. The sternum is much reduced and consists of two regions, the basisternum (BSI) and the furcisternum (FSI). In generalized insects the sternum consists of four regions but among the ants two have been lost either by reduction or fusion and but two remain. The basisternum is a relatively large plate situated between the front coxal extending backward to the furcal pits. It is secondarily divided by a transverse ridge into an anterior and posterior plate. The furcisternum comprises the region to which the furca or sternal apophyses of the endoskeleton are attached. In the prothorax the furcal pits are paired; in the meso- and meta-thorax they are fused into a single cavity.

Mesothorax (Pl. VIII, figs. 1, 3, 4, 5.) The tergum of the mesothorax consists of two regions: a large anterior one, the notum, and a smaller posterior one, the postscutellum. The notum is subdivided into three main divisions: the prescutum, scutum and scutellum. Likewise, the scutum and scutellum are subdivided into smaller divisions. The prescutum (PSC) is a large triangular region separated from the scutum by the notauli (NO). The notauli fuse at the apex of the prescutum, and continue caudad as a median line to the transcutal suture (T, fig. 5) dividing the

scutum in two lateral portions. The scutum (SC) is the most extensive area of the notum and extends laterally to the parapsidal furrows (PF). The parapsidal furrows separate the parapsides from the scutum. The parapsidal furrows are important taxonomic characters widely used in the classification of Hymenoptera. As they are frequently confused with the notauli a complete discussion of these terms has been given elsewhere (Tulloch, 1929). The posterior margin of the scutum is separated from the remainder of the notum by a transverse cleft known as the transcutal suture. Directly behind the scutum is a narrow transverse area, the prescutellum (PRS), a structure present in the more specialized Hymenoptera. It is a part of the scutellum which has become separated from it by a secondary ridge. In *Paraponera* the prescutellum extends clear across the notum but in other forms it becomes reduced to small lateral regions. The scutellum (SCM) is a large convex structure situated behind the prescutellum. The postscutellum (PSM) of the mesothorax is entirely internal and occurs as two separated, flat, scale-like lobes, which occur on each side just caudad of the posterior margin of the scutellum and dorsad of the point of attachment of the hind wing. The postscutellum may extend dorsally along the posterior margin of the scutellum as a very narrow, sclerotized strip, but this is not distinct and the two lateral portions apparently are separated. The posterior region of a wing-bearing tergum is in this species reduced to two lateral plates located underneath the scutellum. They are not visible when viewed from above.

The front margin of the mesothorax is prolonged anteriorly to form a prephragma (PHG) which extends for some distance under and behind the pronotum. It extends as a roll-like thickening along the ventral anterior and lateral margins of the prescutum and scutum, and is flattened to form a thin, plate lobe on each side of the middle of its anterior margin. The postphragma (PFG) of the mesothorax is well developed and much larger than the prephragma. It extends posteriorly nearly to the inner surface of the hind margin of the propodeum (PRO) as a canopy-like, sclerotized plate which tapers posteriorly. Directly above and behind the postscutellar plates there are two regions which appear to be shallow pockets or sacs in the postphragma, one on either side of the middle. In some forms these sacs are connected to the exterior by canals which open between the wing bases. They are possibly glands which never have been recognized.

The pleural region is highly specialized, and consists nearly entirely of a large area divided by a transverse groove into an upper

area, the anepisternum (ANE) and a lower area, the katepisternum (KAT). The pleural suture which in primitive insects extends from the coxal articulation to the wing base and divides the pleuron into episternum and epimeron is entirely lacking; yet the failure of the transverse suture to reach the meso-metapleural suture may indicate its original position. The epimeron (EPM) is reduced to a small region bordering the postero-dorsal margin of the anepisternum. The line of division between the episternum and epimeron is not clear, but study indicates that this is its position. The mesoepisternal and mesosternal sclerites are continuous, there being no complete suture between them. Two short longitudinal lines (Fig. 4) in the sternal region probably indicate the remains of the sterno-pleural suture. The dorsal portion of the mesepisternum borders the front coxal cavities and is, in turn, bordered on its postero-dorsal margin by the mesepimeron. The ventral portion of the mesepisternum is fused with the sternal region, there being no complete suture dividing these regions. The sternum is considered to be divided into two general areas: the basisternum (BS2), a large anterior region, and the furcisternum (FS2), a small posterior region bearing the furca. Their limits cannot be determined owing to lack of sutures; hence the terms are connotative of areas rather than definite sclerites. The furcal pits usually paired in primitive insects are here fused into one common cavity. A median longitudinal groove on the sternum indicates the line of attachment of the apophyses of the mesothoracic endoskeleton. The pleuro-sternal region is modified posteriorly to form the coxal process (CXP) which projects into the mesothoracic coxal cavity from its anterior margin on which the mesothoracic leg articulates.

Metathorax (Pl. VIII, figs. 1, 4). The tergum of the metathorax is divided into an anterior region or notum (MTN) and into a posterior region or postscutellum. The notum is reduced to a narrow transverse plate extending between the hind wings. The postscutellum is posteriorly and laterally indistinguishably fused with the propodeum.

The pleuron of the metathorax consists of one sclerite, the pleuron which is divided into two regions by a secondary suture. The upper region is fused with the postscutellum. The transverse groove which divides the upper from the lower plate of the metapleuron ends posteriorly into a deep depression. This depression is the external evidence of the apodeme which forms part of the endoskeleton of the metathorax. On the lower plate of the metapleuron there is an opening which in this form is slit-like. This

is the opening of the metapleural gland (MG) (erroneously referred to in literature as the metasternal gland). It is peculiar to the ants, and is present in all castes. It appears to be more highly developed in the worker caste. Little is known of its function, though some investigators have suggested it may be a scent organ. The metasternum is considered to be composed of two regions, a relatively large basisternum (BS3) and a smaller furcisternum (FS3).

Propodeum. Technically the propodeum (PRO, fig. 1) is the first segment of the abdomen, the dorsal surface of which, in the more specialized Hymenoptera, has become moved forward and completely incorporated into the thoracic region of the body, its sternum being completely lost. In some species of ants it is provided with spines which are structures of taxonomic value. In this species it is deeply striated. A pair of large spiracles (AI) is located on the lateral regions of the propodeum. Their position similar to the position of the abdominal spiracles indicates at once the abdominal origin of the propodeum.

DIFFERENT TYPES OF ALATE THORAX

The description of the generalized form *Paraponera clavata* may be considered typical for the subfamily Ponerinae. The main differences in the thoracic structure of a typical winged form from each subfamily follow:

CERAPHACHYINAE

Cerapachys manni Crowley

In some respects the thorax of this form appears to be more closely related to the lower Tenthredinoid forms than *Paraponera*, the form selected to illustrate the fundamental type of ant thorax. The structure of the notal region appears to represent a more primitive condition than *Paraponera*; yet, in the pleural and sternal regions, it is more specialized.

This feature of one part of the body becoming more specialized than other parts is here called *differential specialization*. This term is applicable here, as will be shown, for the thorax presents characters at varying stages of specialization.

Prothorax (Pl. IX, figs. 6, 7). The relative position and size of the pronotum (PN) differs somewhat from *Paraponera*, being much larger and more prominent. Consequently, the mesonotum is reduced and is less prominent than in *Paraponera*. Other than its difference in size, it is similar to the other forms. The latero-cervical and sternal regions correspond to those already described.

Mesothorax (Pl. IX, figs. 6, 8, 9, 10). The prescutum is not delimited by notauli, and therefore is part of the complex "prescutum + scutum." The parapsidal furrows (PF) separate the scutum (SC) from the parapsides (PA). The transcuteal suture (T) is present as a distinct cleft. The prescutellum is not separated from the scutellum by a distinct ridge or suture, but by a semi-circular line of rather large indentations. This condition of the prescutellum is suggestive of the primitive condition found in the sawflies. However, the axillary ridge (AXL) which, in other forms reaches to the edge of the notum over the hind wings, assumes a position parallel to the notal surface and curves back toward the scutellum. The scutellum (SCM) is somewhat oval in shape and strongly convex behind. Because of the modification of the prescutellum, it is difficult to detect any parascutellar region. The postscutellum persists as two lobes underneath the posterior margin of the scutellum. Another distinct feature of the notal region is the large tegulae (TG). Usually the tegulae are rather small in the ants, and systematists have used this character as an aid in their separation. In this group the tegulae are very large, somewhat like those of the Mutillidae.

The pleural region consists of a large episternum which is secondarily divided into an upper and lower plate, and a small epimeral region which forms a lobe covering the metathoracic spiracle (S2). The transverse suture across the episternum does not reach the meso-metapleural suture. Its posterior end, therefore, probably indicates the original position of the true pleural suture. The sternal regions are similar to those of *Paraponera*.

Metathorax (Pl. IX, figs. 6, 8). The metanotum (MTN) is a transverse sclerite extending between the wings, and is narrow in the center and wider laterally. The postscutellum is fused posteriorly with the propodeum (PRO) and laterally with the metapleuron. The pleuron is indistinctly divided into an upper and lower region, probably corresponding to the upper and lower plate of the episternum in the mesopleuron. The sternal region is modified so that the identification of the parts is impossible. The general regions are indicated (Fig. 9).

DORYLINAE

Dorylus helvolus L.

In this subfamily only the male is winged, the female being wingless and very rare. The thorax of the male shows the greatest departure from the fundamental type of any of the subfamilies.

Prothorax (Pl. X, figs. 11, 12). The pronotum consists of two triangular areas on either side of the thorax connected anteriorly by a narrow band extending over the front of the thorax. The dorsal posterior lobes are definitely pointed and reach to the tegulae. The opening of the spiracle (SI), which in other forms is covered by the dorsal posterior lobe of the pronotum, is located near the ventral posterior lobe in the region between the two segments, and is not covered by any lobe. Its unusual position is perhaps due to the distortion or unusual shape of the pronotum. The latero-cervical plates are shorter and wider than usual, while the sternal region is considerably reduced.

Mesothorax (Pl. X, figs. 11, 13, 14, 15). The decrease in the size of the prothorax is compensated for by the enlarged size of the mesothorax. Although the specimen considered is a male, the notauli are lacking and the prescutum is indistinguishably fused with the scutum. The parascutellar ridge curves over the tegula, differing in this respect from all the other subfamilies. The prescutellum is reduced to two small lobes, one on either side of the notum. The lobes are not secondarily divided by the axillary ridges. The scutellum extends over the entire dorsum, not being divided into parascutellar regions. The postscutellum is reduced to two narrow strips, one on either side of the notum. The phragmata vary from the usual type, being much smaller in proportion to the size of the mesonotum than in other forms.

The mesopleuron consists of a single large plate, the episternum, there being no indication of a transverse suture dividing it into two plates, or of an epimeral region. The spiracular opening is in the meso-metapleural suture some distance from its usual position in other forms. The mesosternum is very large, and comprises over half of the entire sternal region of the thorax. It is of the usual structure except that the coxal openings are greatly reduced in size.

Metathorax. The metanotum is the only part of this region that can be recognized since the postscutellum and the entire metapleuron is completely fused with the propodeum. It is of the usual structure, and extends between the hind wings.

PSEUDOMYRMINAE

Pseudomyrma damnosa Wheeler

The general appearance of the thorax in this subfamily differs from that of the Ponerinae in that it is more elongate and is compressed dorso-ventrally. The suturing is less complete than in the Ponerinae; yet the limits of the sclerites when present are distinct.

Prothorax (Pl. XI, figs. 16, 17, 18, 19). The pronotum (PN) is a large transverse plate arched in front which tapers somewhat posteriorly and is situated on the anterior margin of the thorax. It extends laterally to the mesopleura, its dorsal posterior angles which are broadly rounded forming lobes covering mesothoracic spiracles (SI). The ventral posterior angles are definitely pointed, and extend but a short distance underneath the thorax. The front margin of the pronotum covers the points of attachment between the head and the internal occipital processes (OP) of the latero-cervicals (LC). The hind margin is concave, and covers the pre-phragma (PHG) of the mesonotum. The latero-cervical region and the sternal regions differ only in shape and size from the corresponding regions in the generalized form and need not be considered here.

Mesothorax (Pl. XI, figs. 16, 18, 19, 20). The greatest differences in structure are found in the mesonotal region. The prescutum (PSC) is not confined entirely by the notauli (NO, Fig. 5), being fused posteriorly with the scutum. Since the posterior limits are absent, this area must be designated as prescutum plus scutum (PRE + SC). The parapsidal furrows (PF) separate the parapsides (PA) from the remainder of the scutum (SC). The posterior margin of the scutum is separated from the rest of the notum by the transcutal suture (T). At the lateral anterior angles of the scutellum (SCM) are two lobe-like structures (PRS) which have been referred to by some taxonomists as the axillae. The results of this study indicate that they are the remains of the prescutellum which in *Paraponera* extended across the notum as a transverse belt. The variation in this region is considered to be indicative of existing relationships in the various types. The scutellum (SCL) is laterally delimited by secondary carina-like ridges. The prescutellum is not separated from the parascutellum by a carina-like ridge as in the Ponerinae.

The pleuron consists of a large episternal region and a very small epimeral region. The episternum is divided into an upper and a lower plate. The epimeron is reduced to a small lobe covering the metathoracic spiracle (S2). The remains of the pleural suture separate the two regions.

The sternal region is little different from that of *Paraponera*. It is divided into two general regions, the basisternum (BS2) and the furcisternum (FS2), the exact limits of each being obscure. Laterally the sternum fuses with the pleuron. This pleuro-sternal region is modified posteriorly to form a coxal process.

Metathorax (Pl. XI, fig. 16). The metanotum (MTN) is reduced to a transverse plate extending between the wings similar to *Paraponera*. The postscutellum (Fig. 17) persists as a groove extending over the tergum. The metapleuron (PL) is reduced to a single plate corresponding to the upper plate of the Ponerinae form. The metapleural gland is well developed and easily visible through the integument. The propodeum is of the usual type.

MYRMICINAE

Manica rubida Latreille

The Myrmicine thorax possesses characters which readily aid in separating it from any of the other subfamilies of ants. Its shape and composition are similar to that of *Pseudomyrma* except for certain minor but outstanding features. The prothorax is very similar to the other forms, except that the invaginations for the occipital processes are much more pronounced.

Mesothorax (Pl. XII, figs. 21, 23, 24, 25). The prescutal and scutal regions are like those of *Pseudomyrma*. The prescutellum (PRS) extends all the way across the notum as a transverse band which is narrowed in the center and widened laterally. It begins to show a tendency to median constriction, a condition preceding to the formation of the two lobes of the *Pseudomyrminae*. Some of the Myrmicines have this region reduced to two lobes, but in general it persists as a transverse band. The axillary ridge (AXL) has disappeared.

In the pleural region the transverse suture across the episterum is very pronounced, existing as a wide, deep groove crossed with oblique striations. An indication of the epimeral region is present, but the epimeral lobe which in all other forms covers the metathoracic spiracle is absent. In this as well as in all other Myrmicines, there is no covering for the spiracular opening. The spiracle itself is much reduced; possibly in some forms it is absent. Its reduced size or possible absence is a convenient character for the identification of this type of thorax.

Metathorax (Pl. XII, fig. 21). The metanotum (MTN) is present as a rather broad transverse band extending between the wings. The postscutellum exists as a narrow region partially fused with the propodeum posteriorly, and completely fused with the pleura laterally. Except in the upper region, the pleura (PL) are completely fused with the propodeum. The metapleural gland is very large, and conspicuous, and indicates the region of the lower plate of the pleuron. The sternum is characterized by the presence of lobes around the furcal pit.

The propodeum is of the usual structure except for the presence of two conical protuberances, one on either side of the body.

DOLICHODERINAE

Dolichoderus bidens L.

The thorax of *Dolichoderus* is in some respects similar to that of the primitive Ponerine forms, especially when viewed laterally.

Prothorax (Pl. XIII, figs. 26, 27, 29). The pronotum is a broad transverse band extending around the front of the thorax to the anterior lateral margins of the mesopleura. The postero-dorsal lobes are bluntly rounded and cover the openings of the mesothoracic spiracles. The postero-ventral angles are pointed and extend a short distance under the prothorax along the anterior margin of the mesosternum. The latero-cervical and the sternal regions are similar to those of *Paraponera*.

Mesothorax (Pl. XIII, figs. 26, 28, 29, 30). The mesonotum is more specialized than in the Ponerinae, the specialization being most noticeable in the prescutellar region. The notauli are lacking, the scutum being indistinguishably fused into a complex called "prescutum plus scutum." The parasides and parapsidal furrows are present and well defined. The transcutal cleft (T) or suture is present and divides the notum into two regions as in *Paraponera*. The prescutellum which in the Ponerine exists as a transverse belt across the entire notum is reduced to two lobes, one on either side of the notum which extend laterally to the lateral margin of the scutellum. A secondary carina-like ridge (AXL) separates the prescutellum into two regions.

The mesopleural region consists of a large plate, the episternum which is divided into an upper and lower plate by a transverse suture; and a smaller plate, the epimeron which covers the opening of the metathoracic spiracle (S2). The failure of the an-katepisternal suture to reach the meso-metathoracic suture probably indicates the limits of the true episternal region. The pleuron and sternum fuse into a general sterno-pleural region, leaving no indication of the original limits. The arrangement of the sternal regions is similar to *Paraponera*.

Metathorax (Pl. XIII, fig. 26). The metanotum is a transverse plate extending between the wings. The postscutellum is reduced to a narrow groove area which is fused laterally to the pleural region. The upper plate of the pleuron (PL) persists while the lower one is fused with the propodeum.

FORMICINAE

Formica sanguinea Latreille

The thorax of this form is similar to that of *Dolichoderus* except in two respects, one in the notal and one in the pleural region. The prothorax differs from the other forms only in shape and size of the various regions.

Mesothorax (Pl. XIV, figs. 31, 33, 34, 35). The prescutellum is reduced to two lobes, one in either side of the notum. The axillary ridge present in *Dolichoderus* is absent in *Formica*. The prescutellar lobes are reduced to a greater extent than in *Dolichoderus*, indicating in this respect a further degree of development. The scutellum is not divided into parascutellar regions as *Dolichoderus*, since the dividing ridge has disappeared.

In the pleural region three regions are easily recognizable, the two plates of the episternum and the small epimeron. The opening of the metathoracic spiracle (S2) is clearly seen beneath the epimeral lobe. The sternal region is similar to other forms. The lower regions of the mesopleuron are nearly completely fused with the metapleuron, a condition found only in this subfamily.

Metathorax. The metanotum is of the usual type, and the post-scutellum is fused posteriorly with the propodeum and laterally with the pleura. The pleural region presents an unusual condition in that the upper plate is present in its entirety while the lower plate is completely fused with the propodeum. The sternal regions present no striking difference from other forms.

THE DIFFERENT TYPES OF WORKER THORAX²

The thorax of the typical wingless workers, being secondary modifications of the alate types of thorax, has but few characters in common. Within a subfamily the workers exhibit striking differences which aid in their taxonomic separation. Characters of the workers widely used in taxonomy are those of the head and pedicel and oftentimes color characters, while thoracic characters have been little used. In the following discussion the thoracic structure of each type is illustrated (Pl. XV) and briefly described.

PONERINAE

Myrmecia sanguinea F. Smith

The workers of the Ponerinae are usually nearly as large as the true females. The thorax is usually divided into three general

² Series of forms intermediate between the winged female and true worker have been considered elsewhere. (Tulloch, 1930 a & b.)

regions: the prothorax, mesothorax, and the metathorax plus propodeum. In some species the metanotum is present and recognizable, but usually the metapleuron and metanotum are indistinguishably fused with the propodeum. Oftentimes the metanotum becomes reduced to a narrow groove resembling a suture, and in such cases taxonomists refer to these grooves as the mesoepinotal suture. The pronotum is usually present in its entirety, and the mesopleuron is separated from the metapleuron by a distinct suture. The mesopleural area is composed entirely of the episternum (EPM), the epimeron having disappeared. The notal region is fused into one general region (MSN).

CERAPACHYINAE

Cerapachys manni Crowley

The entire dorsum of the thorax is not divided by any sutures, all the regions being fused into one complex. Laterally the lower limits of the pronotum are retained as well as the lower portion of the meso-metapleural suture. The pronotum is secondarily divided by a carina into an anterior and posterior region. The presence or absence of this character might be of some taxonomic value. This thorax is one of the most highly developed, and at the same time the most simplified of any found among the insects.

DORYLINAE

Dorylus helvolus L.

The thorax of the worker in this form is as distinctive as that of *Cerapachys*. It is divided into two general regions, the prothorax and a complex of meso- and metathorax and propodeum. The pronotum is entirely distinct from the other structures. The meso-metapleural suture is present in the lower limits of the thorax.

PSEUDOMYRMINAE

Pseudomyra damnosa Wheeler

The thorax of this form is divided into three general regions as *Myrmecia*, and so closely resembles the Ponerine type as to be confused with it. The presence of a well developed metapleural gland visible through the integument is one means of identification, although in some cases this is not a reliable character.

MYRMICINAE

Manica rubida Latreille

In most Myrmicines the entire dorsum is fused into one complex area, but the direction of the secondary striations indicate the limits

of the regions, especially between the pro- and mesonotum. The suture between the pronotum and the mesopleuron is present while the suture between the meso- and metathorax is nearly entirely missing.

DOLICHODERINAE

Dolichoderus bidens L.

In this subfamily the metanotum is usually visible in most species and as well as the upper plate of the metapleuron is retained. The propodeum is large and conspicuous, a feature which aids in its identification.

FORMICINAE

Formica exsectoides Forel

In this species the thorax is divided into three regions of equal size. The pronotum is separated from the mesothorax by a distinct suture. The metathoracic spiracle opens through a tuberculate structure which occurs only in this subfamily. In addition the upper plate of the metapleuron may be distinguished, although it is not definitely delimited by distinct suture. The sutures between the pro- and mesothorax and meso- and metathorax are obliquely distorted forward.

INTERRELATIONSHIPS OF SUBFAMILIES

The general relationship of the various subfamilies of ants to one another have been carefully considered by Wheeler (1923). Basing his conclusions on morphology, paleontology and ethology, he has suggested the following arrangements: The main groups of ants, seven³ in number, may be arranged in three divisions arising from a common ancestral group. In this arrangement the Ponerinae are considered to be the phylogenetic ancestor, giving rise to three main and independent stems. The first stem comprises the Dorylinae and Cerapachyinae, the second includes the Pseudomyrminae and Myrmicinae, while the third contains the Formicinae and Dolichoderinae. This arrangement appears to be generally correct, yet further study may suggest some modifications. This study of the thorax substantiates the arrangement suggested by Wheeler.

In the discussion of the fundamental type of thorax, *Paraponera clavata* was considered, it being one of the primitive Ponerinae.

³ Wheeler (1923) suggested that the genus *Leptanilla* should be given subfamily status. This opinion has been corroborated by G. C. Wheeler (1930).

In general, the thorax of the Ponerines, as exemplified by *Paraponera*, is very generalized, and represents a fundamental type from which the other types may be derived. In both the notal and pleural regions, conditions similar to those found in closely related but less specialized Hymenoptera are present. In many respects the thorax of Ponerines more closely resembles some other Hymenopteran forms than it does the thorax of the highly specialized ants, such as the Formicines.

In studying the interrelationship of any group of insects it is desirable to begin with the earliest ontological stages possible, since by this procedure it is possible to distinguish the primary and fundamental differentiations. In a majority of cases, however, the early stages are not available or, if present, show no differences. In the case of the ants, it is necessary to resort to the adult forms to find significant differences. Since the winged male caste is the most conservative among the ants, and as it varies but slightly throughout the entire group, it is of little value in determining the phylogenetic relationships. It is necessary, therefore, to direct attention to the winged female caste. Moreover, as the winged female caste is the one from which the wingless workers arose at some time during phylogeny, they are the most desirable forms to use in studying their relationships. This discussion of relationships is based upon the thoracic structure of forms considered as types found among the Formicidae.

The particular features of each type of thorax are considered elsewhere. In the Ponerinae it was noted that the prescutellum extended across the notum as a transverse band, and that laterally it was subdivided by the axillary ridge. The prescutum is retained in its entirety in the male owing to the presence of the notauli and the parapsidal furrows which delimit the parapsides. The scutellum is secondarily divided into two lateral areas, the parascutella by a carina-like ridge which is particularly conspicuous when viewed from above. In the mesopleural region the epimeron is present as well as a large episternal region. The metapleural region is distinctly separated from the propodeum by a distinct suture. The variability of these structures aids in determining the relationships of the subfamilies.

The Cerapachyinae and Dorylinae are supposed to have arisen from a common Ponerinae ancestor. In general shape the thoraces of these forms are somewhat similar; yet, in composition they are vastly different. In the Cerapachyinae the thorax presents differentially specialized conditions while in the Dorylinae specialized

conditions are present. The prescutellum of *Cerapachys* is suggestive of the condition found in the sawflies while the position and modification of the axillary ridge is peculiar only to highly specialized Hymenoptera. The tegula is very large and conspicuous, while in the Dorylinae, as well as in all other ants, it is much reduced. The mesonotum is much flattened in both forms, a departure from the Ponerine type. In *Dorylus* the prescutellum is reduced to two small triangular plates, one on either side of the notum. The axillary ridge is lacking, and the position of the parascutal ridge is assigned a distinctive position. In most winged ants it reaches the transeutal cleft at the apparent lateral margin of the notum, but in *Dorylus* it fails to reach the transeutal suture at any point. The pronotum is reduced to a triangular plate completely incorporated within the mesothorax. The mesothoracic and metathoracic spiracles are in an unusual position, being much further down in the pleural region rather than in the general region between the nota and pleura. The latero-cervical region is reduced, being much smaller proportionately than in any of the other types. On the basis of the thoraces of these two forms the similarities are few, being related only in general features. Study of other regions of the body has indicated the general relationships of these groups. They evidently are two groups arising from a common Ponerine stem which have become independently modified to their present conditions.

A second line of development from the Ponerinae leads to the Pseudomyrmacinae and Myrmicinae. These two subfamilies formerly were included into one group, the Myrmicinae. The Pseudomyrmacinae were later separated off as they differed in several minor respects. Both, however, have a pedicel consisting of two well developed segments. From the foregoing it may be noted that these groups are closely related and probably arose from a common ancestral type. In general shape and composition the two thoraces are very similar. The prescutellum is constructed in the middle in *Manica*, a condition preceding the complete construction of this structure into two lobes, as in *Pseudomyrma*. This character is not consistent, however, since some Myrmicines have the prescutellum reduced to two lobes as *Pseudomyrma*; hence, this is not a reliable character for their separation. There is one character which indicates morphological divergence from a common ancestor. In the Pseudomyrmacinae the metathoracic spiracle is covered by a small lobe, the epimeron, while in the Myrmicines the metathoracic spiracle is greatly reduced or absent, and the epimeral lobe is absent. Some

investigators have indicated the position of the spiracle in the Myrmicines; yet this study has indicated that it is either absent or greatly reduced, and never as large and conspicuous as some illustration would seem to imply. The character of the spiracle and its covering are significant characters in the structural differentiation of the thorax.

The Myrmicinae includes a greater variety of forms than any of the other subfamilies. Probably this group will sometime be resolved into other divisions. The genera related to *Pheidolegeton* on the basis of the thoracic structure might be easily separated into a division characterized by having the prescutellum constricted into two triangular lobes similar to the condition found in *Dorylus*. The erection of a subfamily, however, must depend upon distinguishing characteristics from more than one region of the body. Perhaps this thoracic peculiarity mentioned may supplement other distinguishing features from other parts of the body.

A third line of development leads to the Formicinae and Dolichoderinae. They both possess a pedicel consisting of a single highly specialized segment. They are usually separated on the shape and position of the anal orifice. Their thoraces are very similar both in shape and composition. No important differences occur in the notal regions except for the occasional appearance of the axillary ridge in some Dolichoderines and its complete absence in all Formicines. In the pleural regions differences are very evident. In the Formicines the suture between the meso- and metapleuron is nearly obliterated, and the upper plate of the metapleuron is retained in its entirety. In the Dolichoderines the meso-metapleural suture is present, while the upper plate of the metapleuron has disappeared. The plate covering the metathoracic spiracle is well developed in the Formicines and poorly developed in the Dolichoderines.

Assuming that the more specialized ants have arisen from the Ponerines through three lines of development, the following conclusions, based on thoracic structure, have been drawn:

1. The Cerapachyinae and Dorylinae arising from a common stem have become so independently modified that they retain little common to both forms, the thorax of the latter being much more highly specialized than the thorax of the former.

2. The Pseudomyrminae and Myrmicinae are very closely related, yet the latter is slightly more highly specialized.

3. The Dolichoderinae and Formicinae are closely related in general characteristics; yet the thorax of the latter is considerably more highly specialized.

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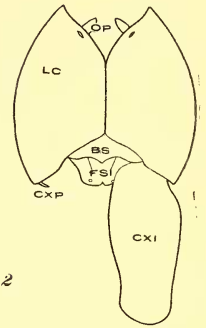
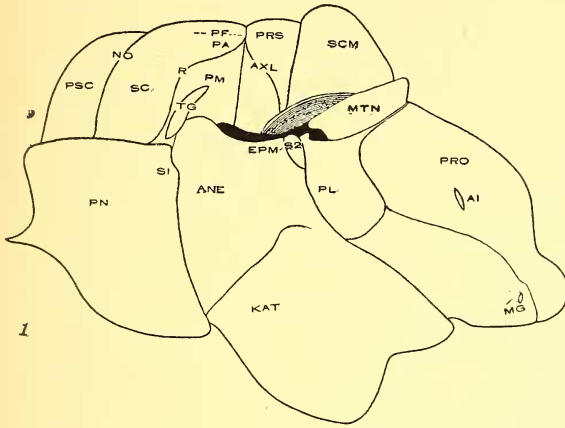
AI	first abdominal spiracle	parascutellum	PAR
ANE	anepisternum	pleural cavity	PC
AXL	axillary ridge	parapsidal fur	PF
BS1, BS2, BS3	basisterna	row	
CXI	coxa of fore leg	PFG	postphragma
CXP	coxal process	PHG	prephragma
EP	episternum	PL	metapleuron
FS1, FS2, FS3	fureisterna	PM	parascutum
KAT	katepisterum	PN	pronotum
LC	laterocervical plate	PRO	propodeum
MG	metapleural gland	PRS	prescutellum
MSN	mesonotum	PSC	prescutum
MTN	metanotum	PSM	postscutellum
OP	occipital process	R	parascutal ridge
PA	parapsis	SI	mesothoracic spiracle
		S2	metathoracic spiracle
		SC	scutum

SCM	scutellum	VW	vestigial wing
T	transeutal	VA	vestigial wing
	suture		articulation
TG	tegula	W	wing insertions

PLATE VIII

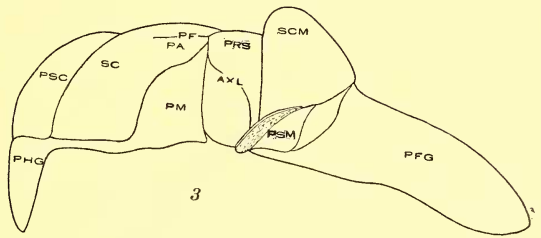
Thorax of *Paraponera clavata* F. Sm.

- Figure 1. Lateral view of thorax.
- Figure 2. Latero-cervical and prosternal region.
- Figure 3. Lateral view of mesonotum.
- Figure 4. Ventral view of thorax.
- Figure 5. Dorsal view of mesonotum.

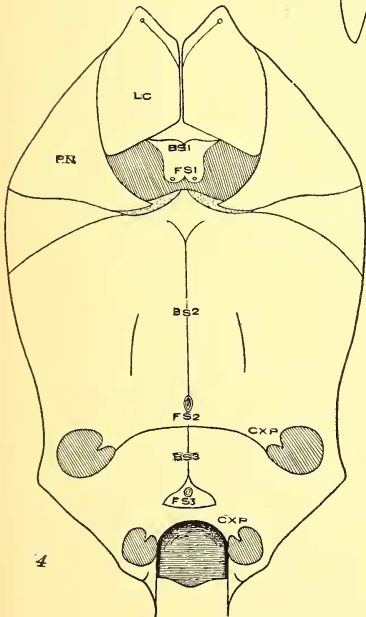


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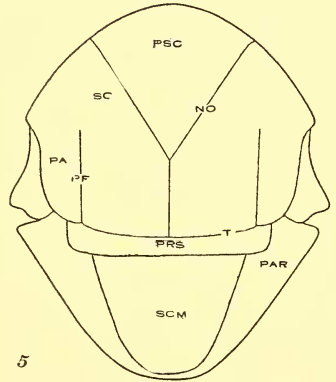
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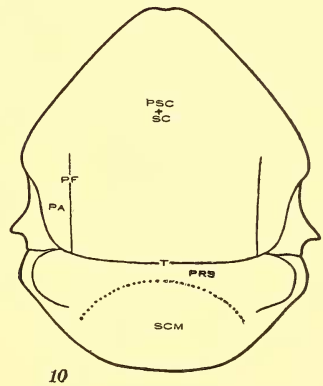
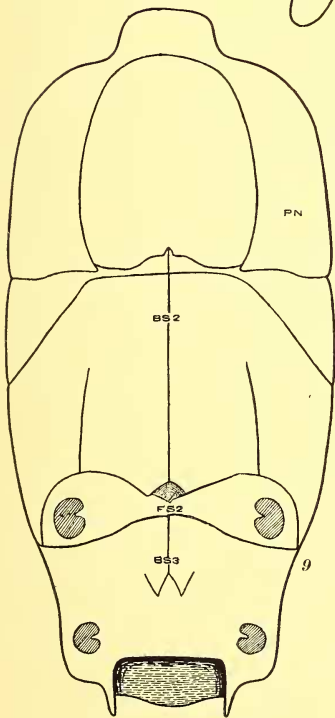
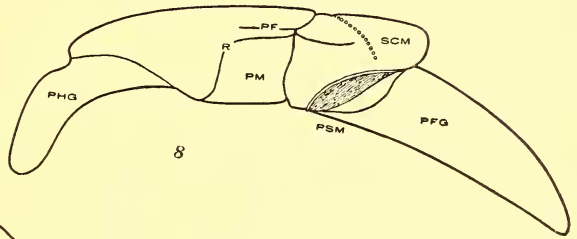
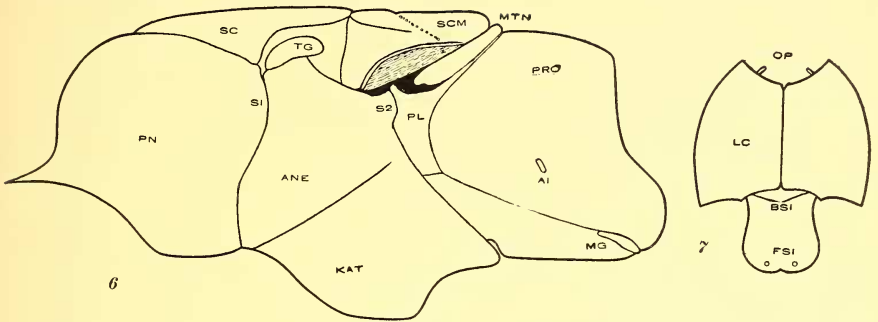


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PLATE IX

Thorax of *Cerapachys manni* Crowley

- Figure 6. Lateral view of thorax.
- Figure 7. Latero-cervical and prosternal region.
- Figure 8. Lateral view of mesonotum.
- Figure 9. Ventral view of thorax.
- Figure 10. Dorsal view of mesonotum.

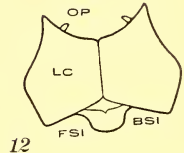
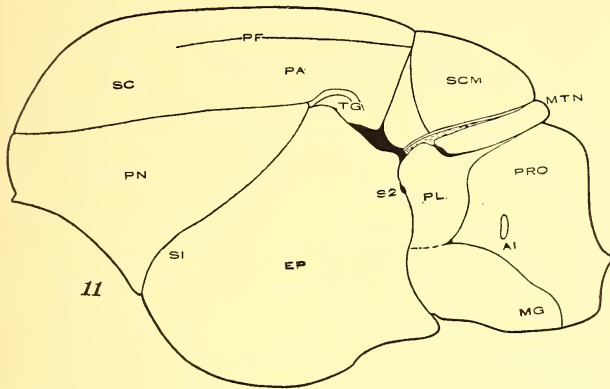


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PLATE X

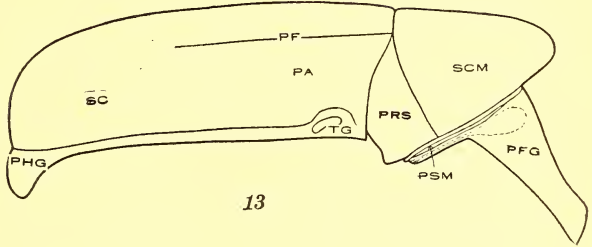
Thorax of *Dorylus helvolus* L.

- Figure 11. Lateral view of thorax.
Figure 12. Latero-cervical and prosternal region.
Figure 13. Lateral view of mesonotum.
Figure 14. Ventral view of thorax.
Figure 15. Dorsal view of mesonotum.

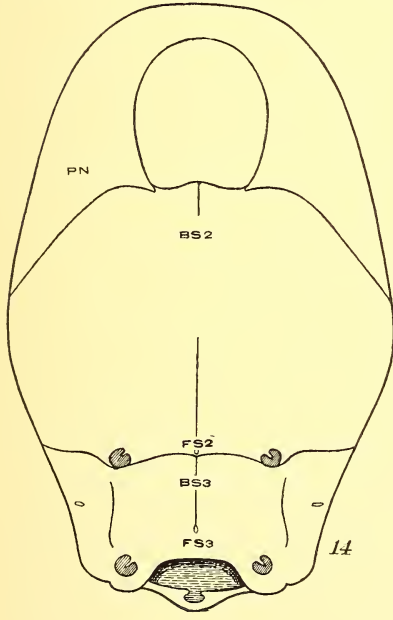


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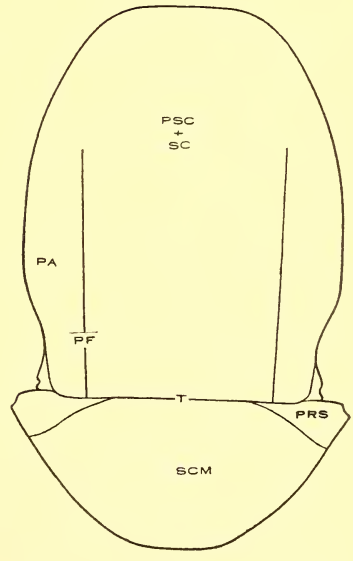
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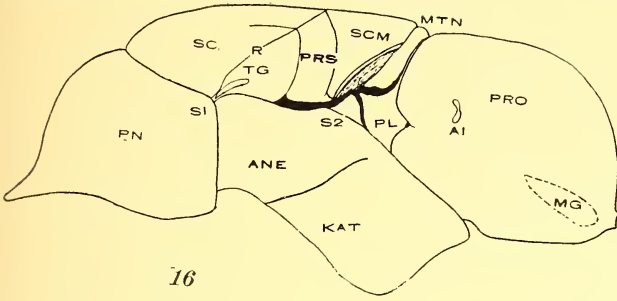


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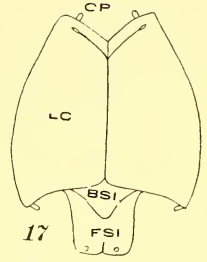
PLATE XI

Thorax of *Pseudomyrma damnosa* Wheeler

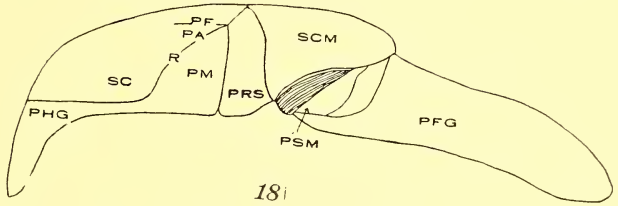
- Figure 16. Lateral view of thorax.
Figure 17. Latero-cervical and prosternal region.
Figure 18. Lateral view of mesonotum.
Figure 19. Ventral view of thorax.
Figure 20. Dorsal view of mesonotum.



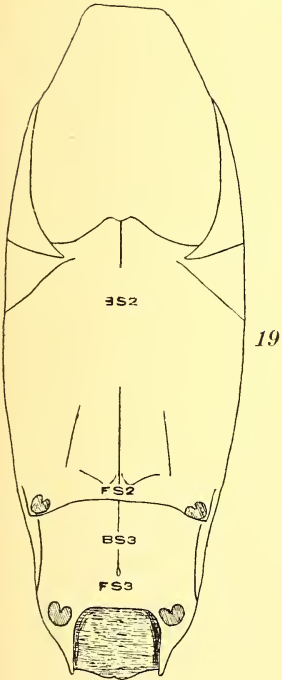
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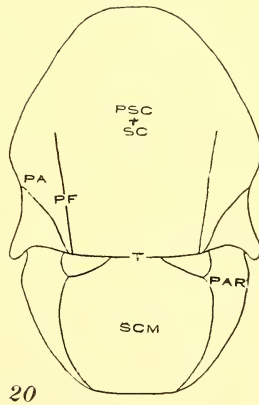
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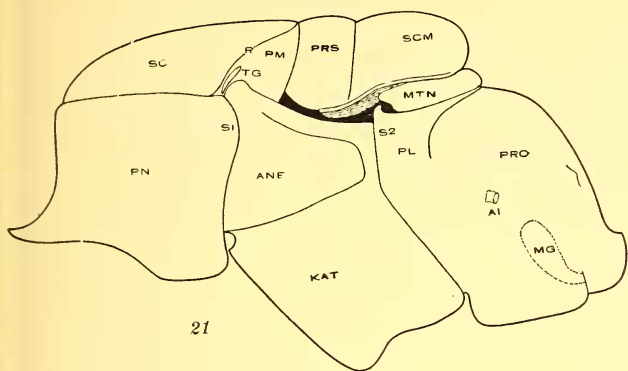


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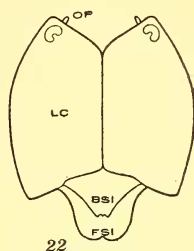
PLATE XII

Thorax of *Manica rubida* Latreille

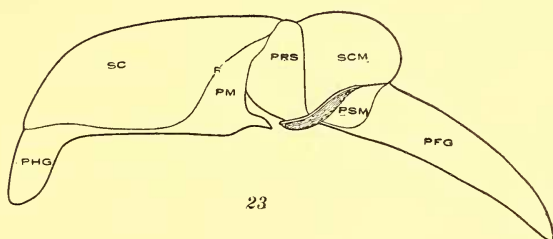
- Figure 21. Lateral view of thorax.
Figure 22. Latero-cervical and prosternal region.
Figure 23. Lateral view of mesonotum.
Figure 24. Ventral view of thorax.
Figure 25. Dorsal view of mesonotum.



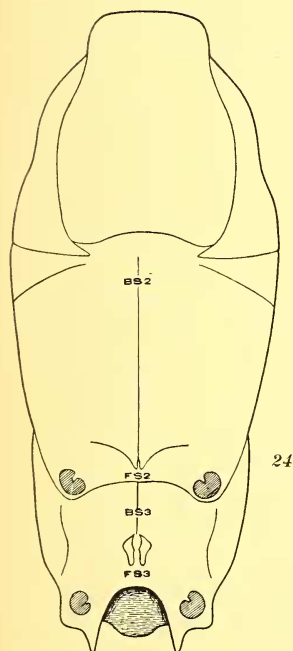
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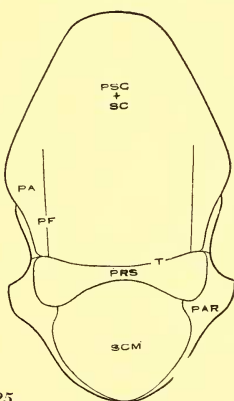
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PLATE XIII

Thorax of *Dolichoderus (Hypoclinea) bidens* L.

- Figure 26. Lateral view of thorax.
Figure 27. Latero-cervical and prosternal region.
Figure 28. Lateral view of mesonotum.
Figure 29. Ventral view of thorax.
Figure 30. Dorsal view of mesonotum.

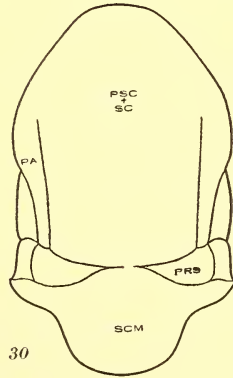
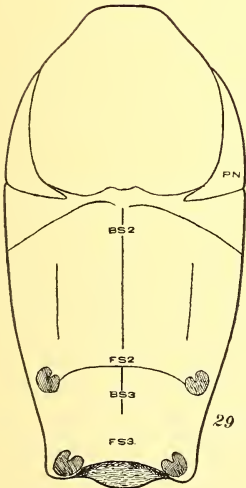
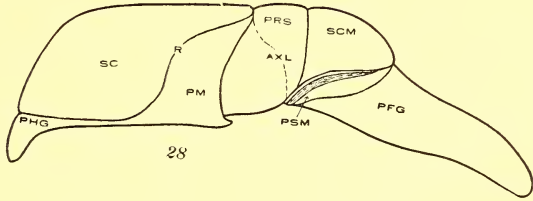
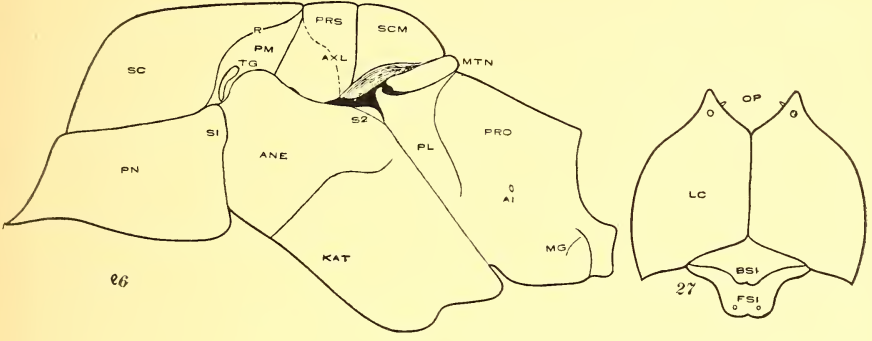
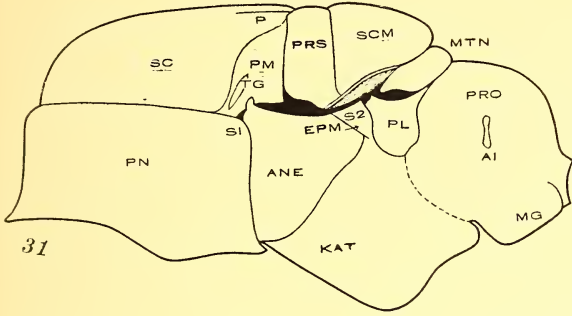


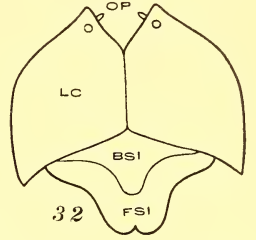
PLATE XIV

Thorax of *Formica sanguinea* Latreille

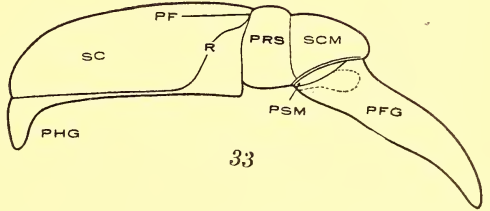
- Figure 31. Lateral view of thorax.
- Figure 32. Latero-cervical and prosternal region.
- Figure 33. Lateral view of mesonotum.
- Figure 34. Ventral view of thorax.
- Figure 35. Dorsal view of mesonotum.



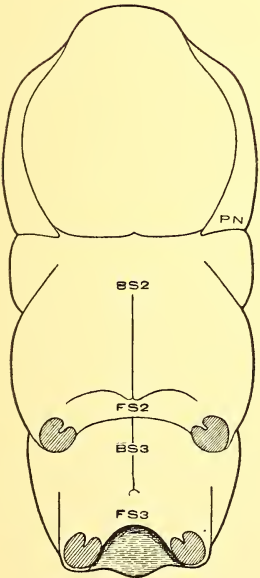
31



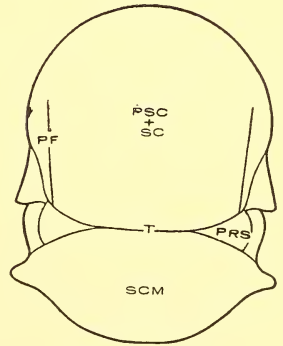
32



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34



35

PLATE XV

- Figure 36. Thorax of *Myrmecia sanguinea* worker.
Figure 37. Thorax of *Cerapachys manni* worker.
Figure 38. Thorax of *Dolichoderus bidens* worker.
Figure 39. Thorax of *Manica rubida* worker.
Figure 40. Thorax of *Pseudomyrma damnosa* worker.
Figure 41. Thorax of *Formica exsectoides* worker.
Figure 42. Thorax of *Dorylus helvolus* worker.